The Reproductive Cycles of Western Redcedar and Yellow-cedar

Province of British Columbia
Ministry of Forests

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PREFACE

British Columbia has 25 native conifer species of which 15 are commercially important and scheduled for reforestation. Tree improvement programs for four of these species are now under way and programs for several other species are planned. A necessary prerequisite for extensive reforestation and tree improvement programs is a complete understanding of the reproductive cycle of each species.

Until 1970, Douglas-fir was the only native species for which the complete reproductive cycle was known. Since that time, studies of the reproductive cycles have been completed for 13 of the other commercially important conifers. These studies include descriptions of vegetative bud and shoot development as they relate to cone initiation, the time and method of cone initiation, predormant and postdormant cone-bud development, pollen development, pollination, and embryo and seed development. Although these studies provide essential details of the reproductive cycles, a more general description of all aspects of the reproductive cycle of a particular species is frequently requested.

This request has resulted in a series of short books concerning the reproductive cycles of several conifers. Serving as ready references for foresters and others concerned with seed production and tree improvement, these books will explain the complete reproductive cycle; provide useful guidelines for cone induction studies; assist in forecasting pollen and seed production; enable more effective pollination; and provide some clues to the causes of poor seed production. In addition, such information should be useful to students of forestry and biology at universities, technical schools and high schools.

This book, *The Reproductive Cycles of Western Redcedar and Yellow-cedar*, is not meant to include a complete literature review. Only the most pertinent and accessible references are cited and listed, providing a source for numerous related reports.

ACKNOWLEDGEMENTS

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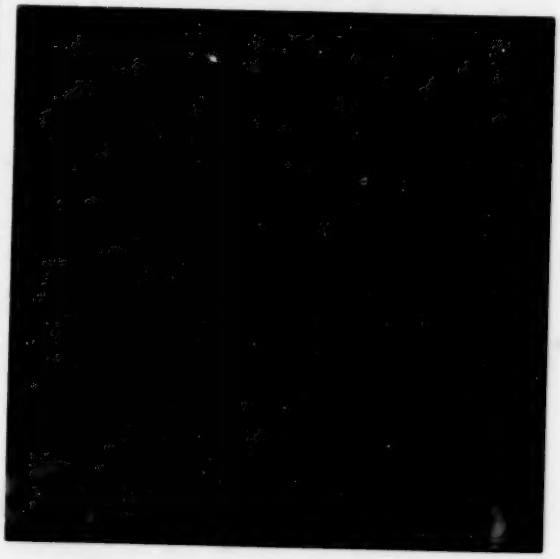
The Reproductive Cycles of Western Redcedar and Yellow-cedar



Introduction

Western redcedar (*Thuja plicata* Donn) and yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) are members of the Cupressaceae, or cypress, family of conifers, which also includes the familiar junipers and many common ornamental trees and shrubs. Members of the cypress family are widely distributed throughout the northern hemisphere, many inhabiting extremely dry desert regions or harsh climates of alpine areas. Several lesser-known genera occur in the southern hemisphere and the tropics. The common name of "cedar" is misleading when applied to *Thuja* and *Chamaecyparis* for it is more accurately applied to the true cedars belonging to the genus *Cedrus*, of which there are no species native to North America.

The Cupressaceae is a large family of 18 genera and over 100 species. Most of the genera are "relics" that were once more diverse and widely distributed than at present, having become reduced to a few species with very limited distribution. Almost all species are characterized by small, scale-like leaves, and none have distinct buds enclosed by bud scales. The seed cones are generally small, often round and woody. A few, however, such as the junipers, have berry-like seed cones. Individuals within some species are monoecious, that is, bear both seed cones and pollen cones. Other species are dioecious, having seed cones and pollen cones borne on separate plants (Foster and Gifford 1974).

Only five species of the Cupressaceae occur in British Columbia: three junipers plus western redcedar and yellow-cedar. These junipers are generally small shrubs except for *Juniperus scopulorum* (Rocky Mountain juniper), which may form a short tree. None of the junipers is harvested for commercial use or used in reforestation. On the contrary, western redcedar and yellow-cedar have high commercial value and are harvested extensively. Planting and modest genetic tree improvement programs for these two species have just begun.

Western Redcedar (*Thuja plicata*)

Thuja, or "arbor-vitae", is a small genus consisting of only six species worldwide. Two species are native to North America: eastern white cedar (*T. occidentalis*) grows in southeastern Canada and the northeastern United States; and western redcedar (*T. plicata*) grows along much of the west coast of Canada and the United States. The other four species occur in China and Japan. One of these Asiatic species, Oriental cedar (*T. orientalis*), is commonly planted as an ornamental tree because of its narrow, conical form.

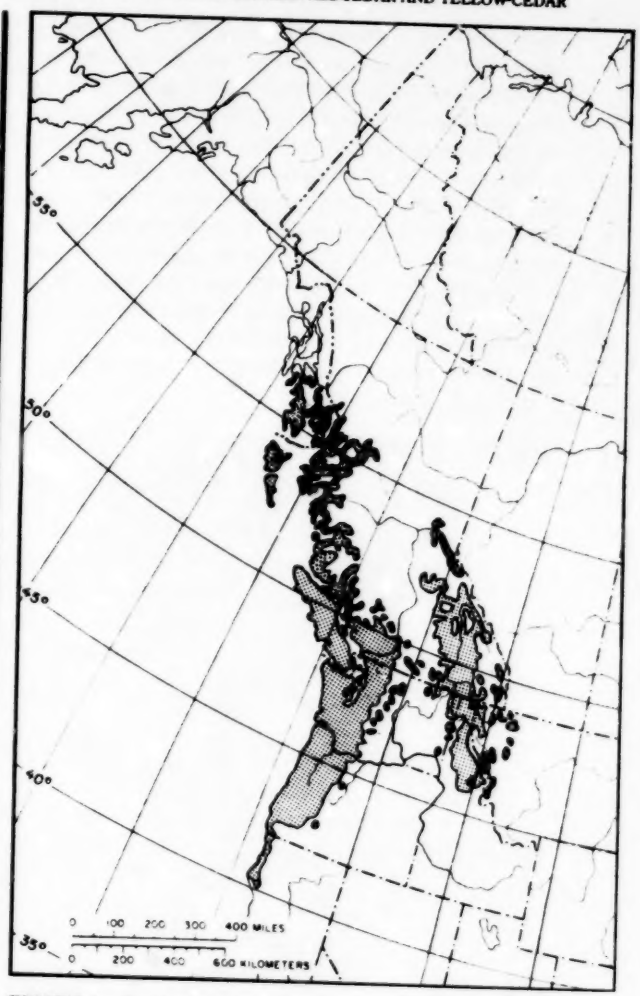


FIGURE 1. Distribution of western redcedar. (Reproduced from Little, 1971.)

Western redcedar grows in the coastal regions from southern Alaska, through British Columbia, and south into northern California. It also occurs in some interior regions of British Columbia, through to the western slope of the Rocky Mountains, and south to Idaho and Montana (Fig. 1). It is, however, usually confined to lower elevations (below 1400 m) and regions having abundant precipitation and humidity (Fowells (compiler) 1965).

Western redcedar is a long-living tree, often up to 800 years, and can, in coastal rain forest, obtain immense size — up to 60 m tall and 2.5 m in diameter. The species is one of the most important timber species in British Columbia. The wood, though low in strength and soft, is very resistant to decay, making it best suited for use as exposed building material, such as shingles, shakes and exterior siding. Its fine, straight-grained wood is also suitable for interior finishing. Historically, the Indians of the Pacific Northwest carved giant totem poles and hollowed out

canoes from this tree, as well as using it for lodges (Hosie 1975).

Although western redcedar is a prodigious cone producer (Fig. 2), each cone contains only a few seeds. These are relatively small, with small seed wings, and are not, consequently, widely disseminated by wind. The tree is generally shade tolerant, its seedlings surviving best in partial shade where they may germinate and grow to maturity. However, because seed growth is retarded in proportion to the density of the shade, western redcedar responds well to removal of competition, and previously supressed individuals may again grow well when competition is removed (Fowells (compiler) 1965).

FIGURE 2. Western redcedar branch with mature seed cones. (X 1)

Although western redcedar's regenerative capacity is moderately good, the tree is being so extensively harvested that natural regeneration is insufficient on many sites. As a result, outplanting of nursery-grown seedlings is becoming essential. At present, seed from low-elevation natural sources is obtained easily, while that from higher elevations is often scarce. In the near future genetic tree improvement programs and seed orchards will be established so that a constant source of high-quality, yet economical, seed is available. Whether seed collections are from wild stands or from seed orchards, it is important to have a thorough understanding of the complete reproductive cycle of this species (Fig. 5).

Yellow-cedar (*Chamaecyparis nootkatensis*)

Chamaecyparis, the white cedar or "false cypress", consists of only seven species worldwide. Three species are native to North America: Atlantic white cedar (*C. thyoides*) which grows in a narrow belt along the east coast and parts of the Gulf coast of the United States; Port-Orford cedar (*C. lawsoniana*) which is the largest species of the genus but restricted to the coastal areas of southern Oregon and northern California; and yellow-cedar (*C. nootkatensis*) which grows mainly along the west coast of Canada and southern Alaska (Fig. 3). The other four species occur in Japan and Taiwan. Some of the oriental species and Port-Orford cedar are planted worldwide as ornamentals (Fowells (compiler) 1965).

Yellow-cedar occurs in a narrow band on the islands

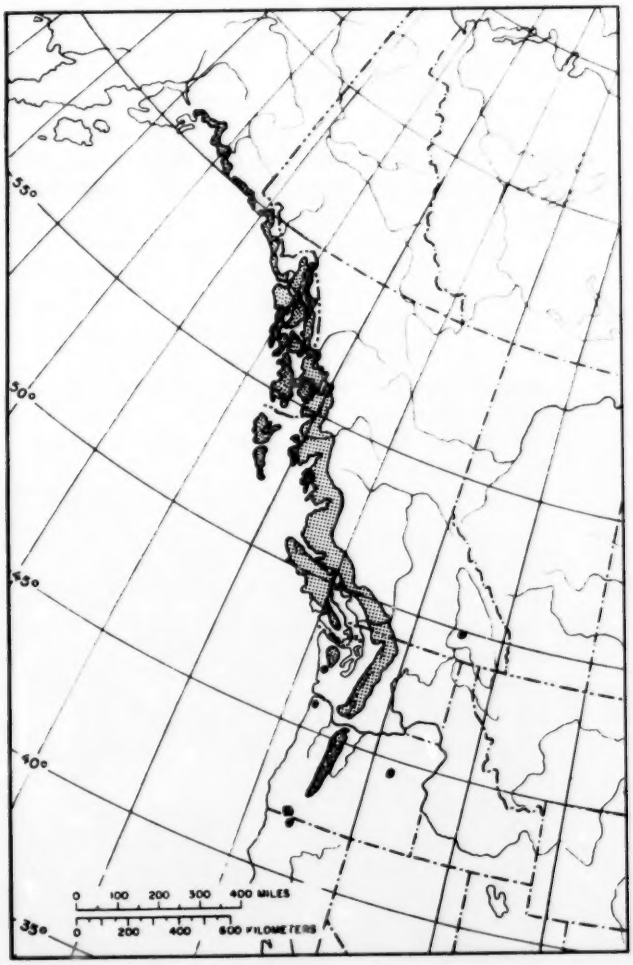


FIGURE 3. Distribution of yellow-cedar. (Reproduced from Little, 1971.)

and along the west coast from Prince William Sound in Alaska to the southwest of British Columbia, and to southern Oregon at higher elevations of the Cascade Mountains. Small isolated stands occur at higher elevations east of the Cascades, in the Olympic Mountains and in northern California. The tree is usually confined to a cool, humid climate where the growing season is relatively short, but winter temperatures are not severe. In the northern part of its range it may grow at sea level, whereas in the southern half of its range it generally grows between 600 and 2300 m elevation.

Yellow-cedar is a slow-growing and extremely long-living tree that may reach 3500 years of age and as much as 53 m in height and 2 m in diameter. It is an important timber species in British Columbia, with wood that is light, hard, strong, close-grained, even-textured and non-resinous. It is prized for boat building and other purposes where its strength and resistance to decay are advantageous. As well, it is excellent for carving, pattern making, and hobby work (Hosie 1975).

Yellow-cedar is not a heavy cone producer, but

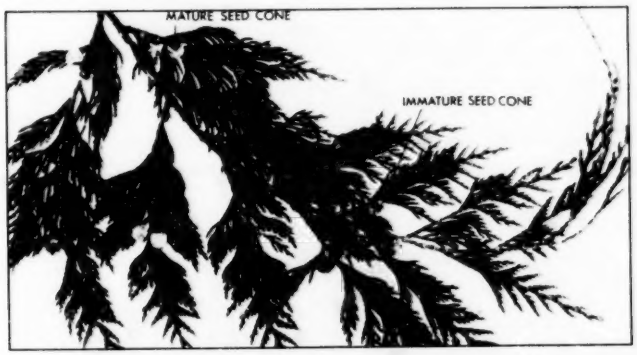


FIGURE 4. Yellow-cedar branch with both mature and immature seed cones. (X 5)

some seed is produced every year. Cones take two years to mature (Fig. 6) and are small, containing few seeds (Fig. 4). The seeds themselves are small, with small seed wings, and are consequently, not disseminated far by wind. Seedlings are less shade tolerant than those of western redcedar or hemlock. Because of its slow growth, yellow-cedar does not compete well with its commonly associated species — Sitka spruce, western hemlock and western redcedar — except in areas less favourable for those species because of poor soil.

The regenerative capacity of yellow-cedar is rather low, especially at the moderate to high-elevation sites where it is commonly harvested. The outplanting of nursery-grown seedlings or cuttings is becoming essential to assure regeneration at current rates of harvest. As for western redcedar, tree improvement programs and seed orchards will be established to provide a constant source of high-quality, yet economical, seed. Because of the two-year maturation period for seed cones, it is even more important than for western redcedar that the complete reproductive cycle of yellow-cedar be understood. First-year and mature second-year seed cones, if collected by error, may not open and seed obtained from them will not germinate. The reproductive cycle includes the events during the 28 months from cone initiation in late spring and early summer, through pollination and early embryo development one year later, to final seed maturity in the fall of the third year (Fig. 6).

The Reproductive Cycle of Western Redcedar

The generally mild coastal habitat of western redcedar contrasts with that of the more severe climate of the interior range. The phenology, therefore, or time sequence of the reproductive cycle, can vary from coastal to interior regions and, in the coastal region alone, from the more severe climate in its northern range to the mild climate in its southern range. The phenology described here is that for western redcedar individuals studied from the middle of the coastal distribution on Vancouver Island (Fig. 1). Even though the phenology varies with geographical distribution, the sequence and details of

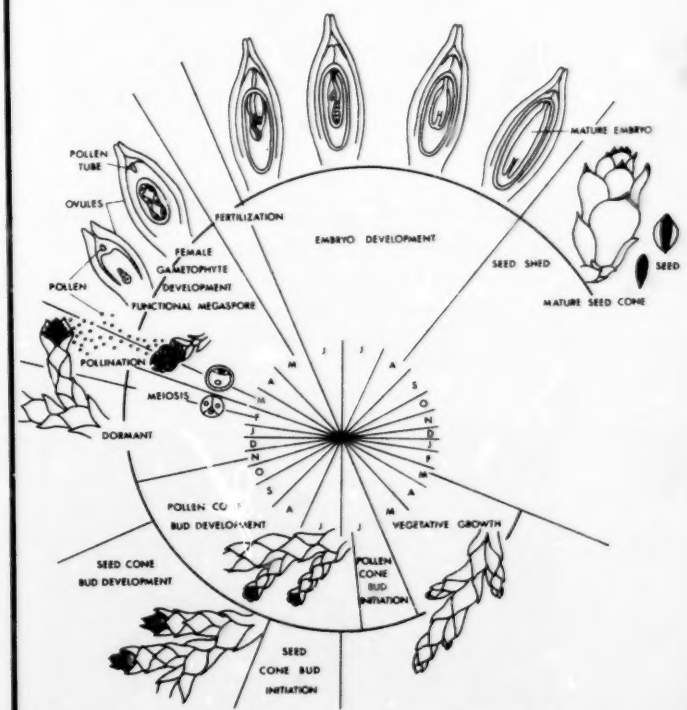


FIGURE 5. The reproductive cycle of western redcedar extends over approximately 16 months from cone initiation to seed maturation.

development remain the same, making a single reproductive cycle valid (Fig. 5). In the colder habitats, developmental events begin later in the spring and stop earlier in the fall, as compared with those in the milder habitats. However, events occurring during the late spring and the summer are little affected.

The reproductive cycle of western redcedar is similar to that of most conifers, and occurs over a period of approximately 16 months. Cone initiation occurs during the spring and early summer, with development arrested for the winter. Pollination, fertilization, and embryo development occur during the following growing season. Seed is mature and shed in the fall of the second season (Fig. 5).

The Reproductive Cycle of Yellow-cedar

The extensive range of over 2500 km along the west coast suggests that the growing season and phenology of yellow-cedar would vary considerably at the extremes of this range. However, since the northern limit of its range is near sea level and its southern limit rises to 2300 m, the growing season, except at very high elevations, lasts approximately 150 days from mid-April through mid-September. Within this range, the phenology does not generally vary by more than one month at the beginning and end of the growing season. The important events that occur during the middle of the growing season, in late spring and early summer, will take place at essentially the same time throughout its range. Variation in phenology, however, does not alter the sequence and details of development so that a general reproductive cycle for yellow-cedar is valid (Fig. 6). The phenology described here is for yellow-cedar individuals studied from south of the middle of the range, in southern British Columbia at 600 m, and on Vancouver Island near sea level.

The reproductive cycle of yellow-cedar occurs over 28 months and is spread over three growing seasons. Cone initiation occurs in the late spring and early summer, pollination occurs the following spring, and fertilization follows soon after. Embryo development begins the year of pollination, stopping late in the summer and completing in the following spring and summer. Seed is shed in the fall of the third season (Fig. 6).

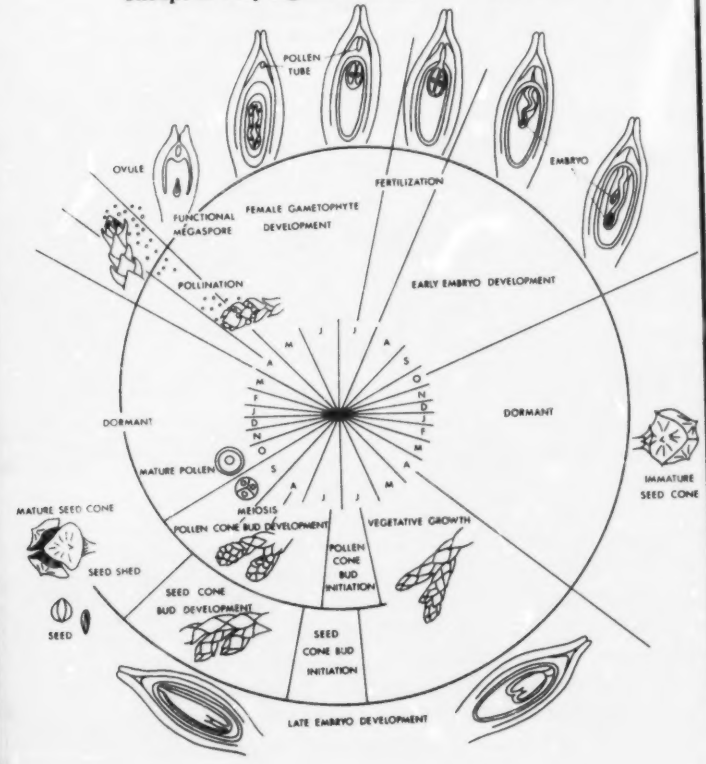


FIGURE 6. The reproductive cycle of yellow-cedar extends over approximately 28 months from cone initiation until seed maturation.

Shoot Development

Western redcedar and yellow-cedar have very similar shoot development. No distinct buds enclosed by bud scales are formed (Fig. 7). Instead, the apical meristem, or apex, of each shoot is enclosed by scale-like leaves at various stages of development (Fig. 8). The embryonic leaves close to the apical meristem are those formed most recently. As leaves enlarge and mature they become further removed from the apical meristem (Fig. 8), which continues to

FIGURE 7. Vegetative shoot tip of yellow-cedar showing decussate leaves, three lateral branches, and no bud scales. (X 15) LEFT

FIGURE 8. Median longitudinal section of a yellow-cedar shoot tip, as in Figure 7, showing the apical meristem (APEX), leaves (L) and lateral branches (LB) at various stages of development. (X 35) RIGHT

form new stem tissue and leaves from early spring until fall. Shoot growth and leaf initiation are slow early and late in the growing season, and more rapid during late spring and early summer.

The scale-like leaves occur in two opposite rows, each row at a 90° angle to the other. This is a "decussate" leaf arrangement. Two leaf primordia are initiated at the same time from opposite sides of a small apical meristem (Fig. 9). This reduces the size of the apical meristem at first (Figs. 9, 10), but it then enlarges (Fig. 9) and a second pair of leaf primordia is initiated at a 90° angle to the previous pair. The time interval between initiation of successive pairs of leaves is from one to several days, and is shortest during late spring and early summer when shoot elongation is most rapid.

Lateral branches are initiated in the axils of certain leaves, that is, in the area just above the juncture of the leaf with the stem. A lateral branch begins as a small apical meristem that enlarges and initiates a series of decussate leaves in the same manner as the terminal apex. A lateral branch primordium is usually initiated in the axil of one leaf in every second to fourth pair of leaves (Fig. 8). The leader shoot and any other large or erect lateral shoots initiate lateral branch primordia in the axils of leaves on all sides of the stem. Consequently, branching on these shoots is three dimensional. Most lateral branches, however, especially those that are pendant, initiate lateral branch primordia only in the axils of leaves on the sides of the shoots rather than in the axils of leaves on the upper and lower surfaces. As a result, branching is two dimensional, forming flattened sprays. Lateral branch primordia are also initiated more frequently in leaf axils on the distal side of the branch (that side nearer the main shoot apical meristem). This results in an asymmetrical branching pattern with most lateral branches occurring on the distal side of a shoot (Figs. 2, 7).

The separation between successive leaf pairs (the "internodal elongation") is wider and leaf bases are longer on vigorous shoots than on smaller lateral shoots.

FIGURES 9, 10. Median longitudinal sections of yellow-cedar shoot tips showing the apical meristem (APEX) just before the initiation of leaf primordia (LP) (Figure 9) and just after initiation of two leaf primordia (Figure 10). (X 200)

Cone Initiation

The method of cone initiation is similar in western redcedar and yellow-cedar. Cones develop at the tips of short vegetative shoots during the late spring or early summer (Figs. 5, 6), and are not enclosed by bud scales (Figs. 18-25). Development begins when a vegetative apical meristem, which has been initiating leaves, undergoes a transition to become a reproductive apical meristem, which in turn initiates the reproductive structures of the pollen cone or seed cone. The transition involves metabolic changes, as yet not well understood, that alter the direction of development of the apical meristem. First the rate of cell division increases in the apical meristem, followed by a change in its size and shape. New types of leaf-like organs are then initiated, instead of scale-like leaves.

Pollen-Cone Initiation

In both western redcedar and yellow-cedar, pollen cones develop on less vigorous lateral branches, usually in lower regions of the crown, some distance back from more vigorous lateral branches. Pollen-cone initiation usually occurs at the tips of unbranched, pendant shoots that have grown for one or more years

FIGURE 11. Median longitudinal section of yellow-cedar apex undergoing transition from a vegetative to a pollen-cone apex. A lateral apex (LA) has been initiated from the terminal apex (TA). (X 300)

and have formed many leaves (Figs. 18, 22). Transition from a vegetative to a reproductive apical meristem occurs over a few days. As the apical meristem enlarges, there is a delay in the rate of leaf development and a series of decussate microsporophylls is initiated. A short stalk develops between the last leaves and first microsporophylls. No intermediate structures form during the transition period.

In western redcedar, pollen-cone initiation begins in early June with the pollen-cone apical meristem initiating four to five pairs of microsporophylls before development stops, usually about mid-July.

Pollen-cone initiation in yellow-cedar is similar to that in western redcedar except that, during the transition period, a lateral apical meristem arises from the terminal apical meristem (Fig. 11). The terminal apical meristem then initiates decussate

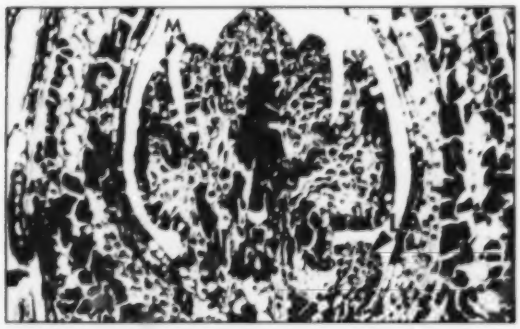


FIGURE 12. Median longitudinal section of a yellow-cedar pollen cone during microsporophyll (M) initiation. The small lateral apex (LA) is at the base. (X 125)

microsporophylls before stopping development about mid-August. The lateral apical meristem may initiate a few leaves and then become dormant, remaining as a very small shoot at the base of the pollen cone (Fig. 12). The function of this tiny lateral branch is to regenerate a new vegetative shoot the next spring after pollination, when the pollen cone dries and falls from the shoot (Fig. 13). This process allows a shoot to form a pollen cone more than once, thus increasing

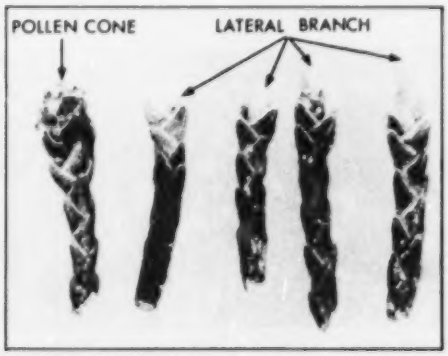


FIGURE 13. Development of the lateral branch after the pollen cone has fallen from the shoot. (X 5)

the number of potential shoots on which pollen cones can be initiated. In western redcedar this does not occur: once its lateral shoots produce a pollen cone, the growth of those lateral shoots ends.

Seed-Cone Initiation

In both western redcedar and yellow-cedar seed cones develop near the tips of vigorous lateral branches, usually in upper regions of the crown.

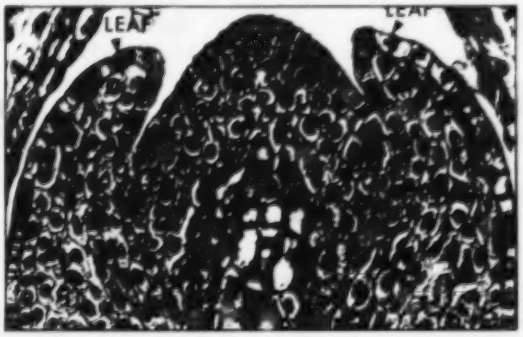


FIGURE 14. Median longitudinal section of a yellow-cedar apex undergoing transition from a vegetative to a seed-cone apex. (X 220)

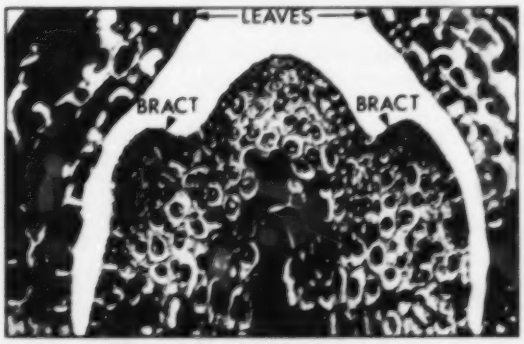


FIGURE 15. Median longitudinal section of a yellow-cedar seed cone apex during the initiation of the first pair of bract-scales (BRACT). (X 220)

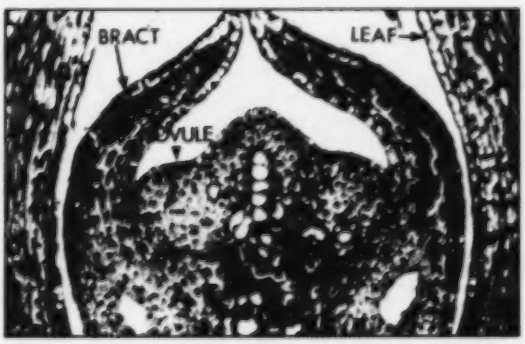


Figure 16. Median longitudinal section of a yellow-cedar seed cone showing the initiation of the first two ovules, each in the axil of a bract-scale (BRACT). (X 150)

These cones are initiated terminally on short lateral shoots that developed only a few weeks earlier and produced only a few pairs of leaves (Figs. 20, 24).

Transition from a vegetative to a reproductive apical meristem is similar in both species. After the short lateral vegetative shoot has produced several pairs of leaves, the apical meristem enlarges greatly (Fig. 14) and begins to initiate decussate pairs of leaf-like organs (Fig. 15). Each organ consists of a fused bract and ovuliferous scale. Soon after a pair of bract-scales is initiated, one to three ovules begin to develop in the axil of each (Figs. 16, 17). When all bract-scales and ovules have been initiated (usually by the end of August), the apical meristem stops

FIGURE 17. Scanning electron micrograph of a western redcedar seed cone showing the bract-scale (BRACT) and the developing ovules after the subtending bract-scale was removed. (X 100)

development (Figs. 21, 25). In neither species is a lateral branch bud formed at the base of the seed cones to regenerate the shoot after the seed cones are shed.

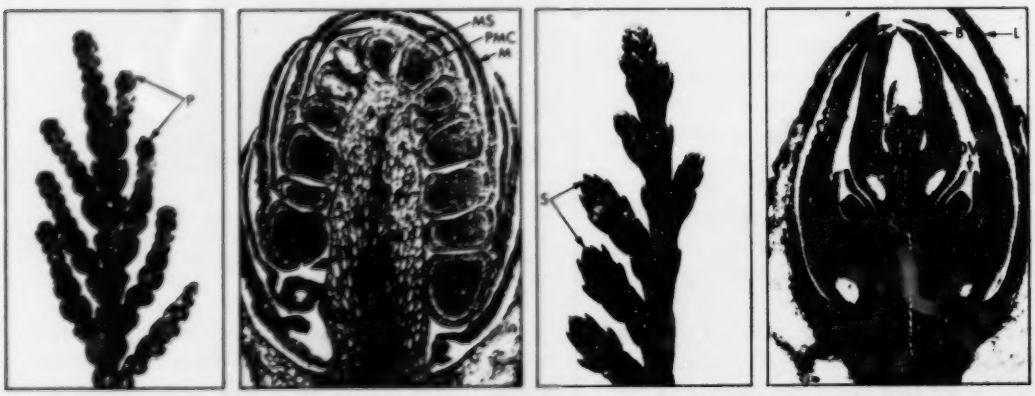
Cone Development Before Dormancy

Before dormancy western redcedar pollen cones initiate between 8 and 10 microsporophylls, which range in colour from brown to black (Fig. 18). Each microsporophyll bears three red microsporangia. These microsporangia contain hundreds of pollen mother cells (Fig. 19), which undergo no further development until after dormancy. Dormant pollen cones are globose and only 2 to 3 mm long, with a 1 mm stalk. The dark microsporophylls are nearly covered by the leaves below (Fig. 18).

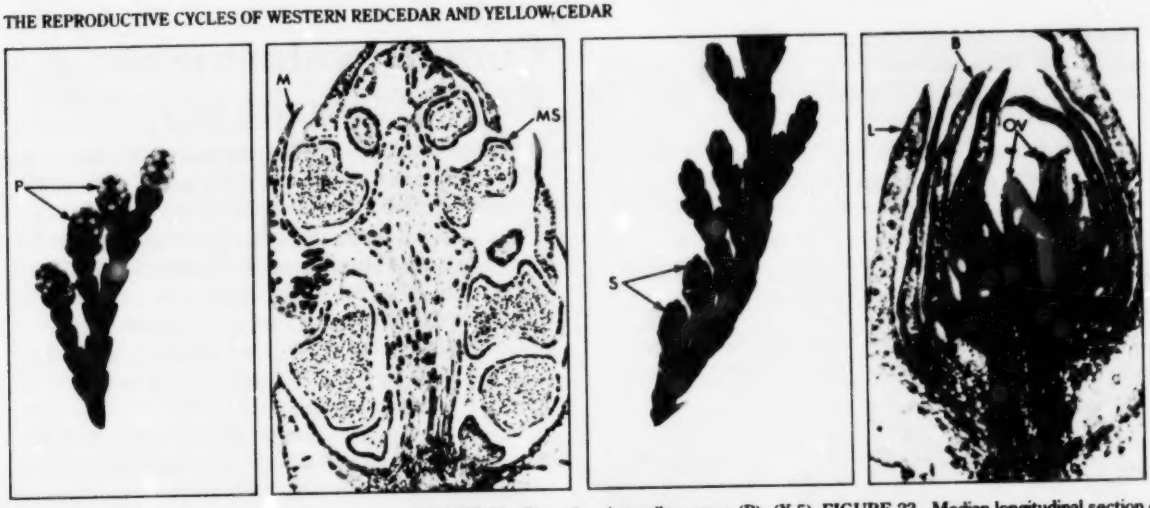
Western redcedar seed cones initiate 8 to 12 bract-scales. These are mostly green with brown to black pointed tips (Fig. 20). Basal bract-scales bear only rudimentary ovules; middle bract-scales bear three ovules; distal bract-scales bear two ovules. Dormant seed cones are globose and 2 mm long (Figs. 20, 21). The shoot subtending the seed cone bends up, raising seed cones above adjacent vegetative shoots.

Yellow-cedar pollen cones initiate 10 to 12 microsporophylls before dormancy (Fig. 22), and each microsporophyll bears three yellow microsporangia. Unlike western redcedar, pollen mother cells of yellow-cedar continue to develop, and undergo meiosis in late August when each cell forms four 1-celled pollen grains before dormancy (Fig. 23). Meiosis and pollen development cause the microsporangia to swell and become exposed, which gives the dormant pollen cones a distinctive yellow colour. Microsporophylls remain small and green or brown. Dormant pollen cones are approximately 3 mm long (Fig. 22).

Yellow-cedar seed cones initiate 6 to 8 bract-scales, which, though green, are larger than the few basal leaves on the same shoot (Fig. 24). Each bract-scale has usually three axillary ovules. Because the cone axis is shorter than in western redcedar, the axillary



FIGURES 18-21. Dormant western redcedar cones. **FIGURE 18.** Shoot bearing pollen cones (P). (X 4) **FIGURE 19.** Median longitudinal section of a pollen cone showing microsporophylls (M) and the microsporangia (MS) containing pollen mother cells (PMC). (X 40) **Figure 20.** Shoot bearing seed cones (S). (X 4) **FIGURE 21.** Median longitudinal section of a seed cone showing ovules (OV), bract-scales (B), and basal leaves (L). (X 35)



FIGURES 22-25. Dormant yellow-cedar cones. **FIGURE 22.** Shoot bearing pollen cones (P). (X 5) **FIGURE 23.** Median longitudinal section of a pollen cone showing microsporophylls (M) and the microsporangia (MS) containing pollen. (X 38) **FIGURE 24.** Shoot bearing seed cones (S). (X 5) **FIGURE 25.** Median longitudinal section of a seed cone showing ovules (OV), bract-scales (B) and basal leaves (L). (X 45)

ovules appear to be borne on a flattened receptacle (Fig. 25). Dormant seed cones are 3 mm long and are pointed (Fig. 24).

Cones of both species are identifiable on dormant shoots, so estimates of potential seed-cone crops can be made at least 13 months before western redcedar cones are mature, and 25 months before yellow-cedar seed cones are mature (Figs. 5, 6). Many factors can cause seed cones to abort during this time, or can prevent either pollination or normal seed development. All that can definitely be said, based on cone-bud counts, is that if few or no cone buds are present, the cone crop will be small or nil; if cone buds are present, it is possible that there will be a cone crop.

Enhancing Cone Initiation

Within the Cupressaceae, cone induction in seedling and juvenile trees and cone enhancement in sexually mature trees, is relatively easy and inexpensive, especially when compared with species within the Pinaceae. Because species within the Cupressaceae undergo free growth throughout the growing season, and do not have buds with bud scales and complex, fixed cycles of bud development, the period of cone initiation is less precise than in the Pinaceae. In the Cupressaceae cones can be induced at times other than the normal time for cone initiation. Trees grown in a greenhouse or growth chamber, out of phase with trees growing in their native habitat, can be induced to "flower" at almost any time of the year, as long as they are not dormant (Fig. 26). However, the greatest effect is obtained if trees are treated under environmental conditions similar to those found in nature, at what would be the normal time of cone initiation for this species (Figs. 5, 6).

The common treatment used is a foliar spray of gibberellin A_3 at a concentration of 100 mg/L in an aqueous 0.1% Tween-20 solution. Trees are sprayed

FIGURE 26. One-year-old yellow-cedar trees showing the untreated control tree on the left; and on the right, the treated tree which was sprayed twice weekly with 100 mg/L-gibberellin A_3, from June until August. Many seed cones (S) and pollen cones (P) have been initiated on the treated tree.

until the foliage drips and sprayings should occur twice weekly for about six weeks. Good results have been obtained using this technique on 1- to 3-year-old seedlings and young trees of both species. Cones develop normally if treatments occur early enough for cones to differentiate fully before dormancy. It has

been shown in western redcedar that, for normal cone development to occur, a five- to seven-week period of short days preceding a period of long days must follow cone differentiation. An even greater number of cones develop normally if the short-day period is accompanied by cold temperatures and the following long-day period by warm temperatures. This most closely simulates the natural overwintering conditions for cone development. Similar treatments would be applicable for yellow-cedar (Pharis *et al.* 1969).

It has been demonstrated in both species that gibberellin A_3 treatment over long days (e.g. 16 hours) increases the proportion of pollen cones induced; and treatment over short days (e.g. 8-10 hours) increases the proportion of seed cones produced (Pharis and Morf 1970; Owens and Molder 1977). This is not surprising because, under natural conditions, both species initiate pollen cones over long days while day length is increasing, and seed cones over long days while day length is decreasing (Owens and Pharis 1971; Owens and Molder 1974). The photoperiodic requirement appears to be the increase of daylengths for pollen-cone initiation, and the decrease of daylengths for seed-cone initiation — not the number of long days and short days, respectively.

Pollen cones induced on juvenile trees produce viable pollen that, when applied to gibberellin A_3-induced seed cones, produce normal, viable seed. However, because gibberellin A_3 may induce such large numbers of cones, a higher proportion of cones may abort than occurs under natural conditions (Owens and Molder 1977).

Stress treatments such as girdling and root pruning, which are commonly used in conjunction with non-polar gibberellin A_4, A_7 and A_9 to induce cones in the Pinaceae, do not have an effect when used in conjunction with gibberellin A_3 in the Cupressaceae. Furthermore, the non-polar gibberellins do not induce cones in the Cupressaceae, with or without stress; and the polar gibberellin A_3 is ineffective for cone induction in the Pinaceae, with or without accompanying stress treatments.

Individual trees may show variable responses to cone-induction treatments. Original reports should be consulted before large-scale induction trials begin (Owens and Pharis 1971; Owens and Molder 1977).

Pollen Development

Pollen development is essentially the same in both western redcedar and yellow-cedar (Fig. 27), even though western redcedar forms pollen after winter dormancy and yellow-cedar forms pollen before winter dormancy.

The pollen sacs, or microsporangia, form hundreds of large, angular, pollen mother cells (Figs. 27*A, B*). Each of these cells undergoes meiosis, the special form of cell division that produces four microspores, or a "tetrad" (Fig. 27*C*). Each microspore contains 12 chromosomes, or half ("haploid") the original number. In western redcedar meiosis occurs in late February after winter dormancy; in yellow-cedar it occurs in late August before winter dormancy (Figs. 5, 6). In both species, pollen develops during the three to four weeks after meiosis occurs. (The time of meiosis can be estimated through observation of the pollen cones, whose pollen sacs and pollen cones enlarge rapidly during the division process.)

Microspores are first angular but soon round out, developing a thick wall of two distinct layers: a thin, smooth inner layer ("intine"); and a thick outer layer ("exine") (Fig. 27*E*). The outer surface of the exine

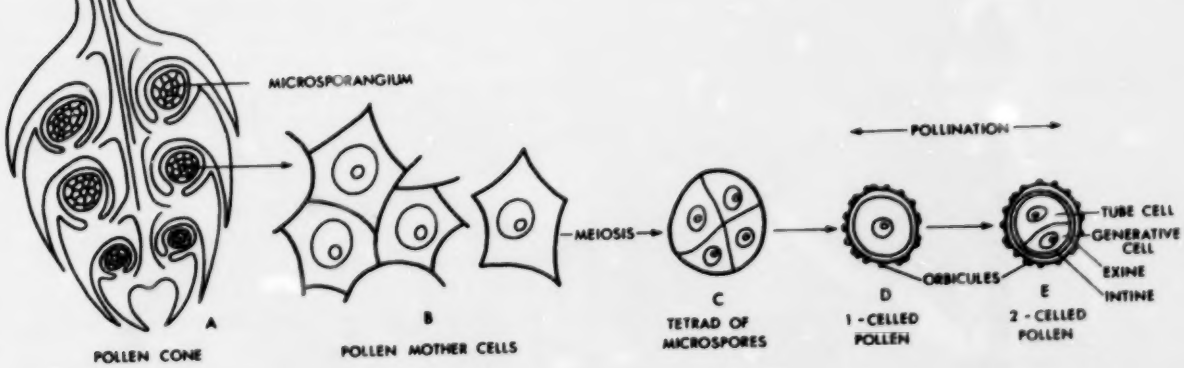


FIGURE 27. Pollen development in western redcedar and yellow-cedar. The entire development occurs after winter dormancy in western redcedar and before winter dormancy in yellow-cedar.

becomes finely sculptured and many tiny spherical orbicules are deposited on its surface. The orbicules, which result from the degeneration of the inner layer of the microsporangium (or "tapetum") occur singly or in small clusters and are less abundant in western redcedar than in yellow-cedar (Fig. 28). Pollen with orbicules deposited on the surface is characteristic of the Cupressaceae.

Within the developing pollen grain of western redcedar, and before the pollen is shed, the microspore (Fig. 27*D*) divides to form a large tube cell and a smaller generative cell (Fig. 27*E*). In yellow-cedar this division may occur either before the pollen is shed, as in western redcedar, or after the pollen is shed. In both species the generative cell divides just before fertilization, forming two male gametes; and the developing pollen stores food as oil droplets rather than starch.

FIGURE 28. Scanning electron micrograph of western redcedar pollen. (X 1050)

FIGURE 29. Stained western redcedar pollen. (X 700)

FIGURE 30. Scanning electron micrograph of yellow-cedar pollen. (X 1300)

FIGURE 31. Stained yellow-cedar pollen. (X 700)

Pollen dries as it matures within the microsporangia, and this drying causes the spherical pollen to become irregular in shape. Dry western redcedar pollen, because of its thinner wall, becomes more indented and irregular (Figs. 28, 29) than the thicker-walled dry yellow-cedar pollen (Figs. 30, 31). Mature, dry pollen of both species averages from 20 μ m to 30 μ m in diameter.

Pollination

The pollination mechanism is essentially the same in western redcedar and yellow-cedar (Owens and Molder 1980; Owens *et al.* 1980). Differences occur only in the time of pollen formation and pollination (Figs. 5, 6), and in the shape and position of ovules in the seed cones. Pollination in both species lasts for about one week but may extend over two to three weeks depending on a tree's location, and from one to two months at the distribution extremes of each species. In British Columbia, western redcedar may begin pollination as early as mid-February in mild coastal areas, and as late as early April at higher elevations. Pollination in March is most common. Yellow-cedar may begin pollination in late March in coastal areas, and in late April at higher elevations and northern limits of its range.

Western redcedar pollen cones enlarge when dormancy ends, and the microspore mother cells undergo meiosis almost immediately. Mature pollen is formed within about three weeks. Yellow-cedar pollen cones, however, enlarge before dormancy and contain fully formed pollen. In both species the cone axis elongates, separating the microsporophylls, and the microsporangia dry and split open, releasing the powdery pollen.

All ovules are initiated before dormancy and develop into small flask-shaped structures in the axils of bracts. In western redcedar the ovules are flattened and buried deeply between bracts (Fig. 33); in yellow-cedar, ovules are more angular and perched on a flattened receptacle at the tip of the cone (Fig. 34).

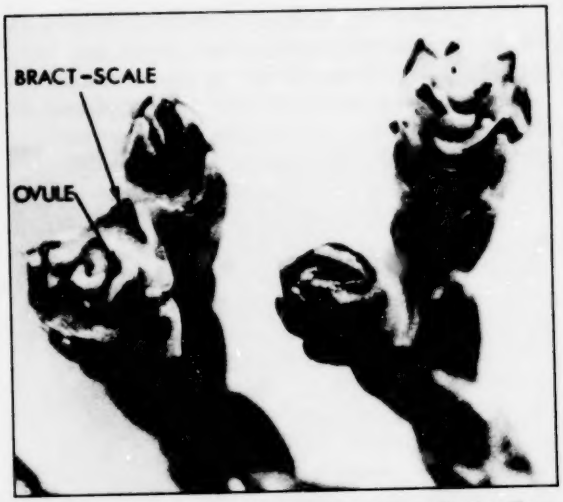


FIGURE 32. Western redcedar cones opening at pollination. Two cones are still closed. Ovules are visible between bract-scales (B). (X 7)

When dormancy ends, the seed cones enlarge slightly and bend upward, their bracts opening out to expose the ovules and the open micropyles (Fig. 32-34). This process may occur with only a few days of warm temperatures, though not all cones on a branch will open at the same time (Fig. 32). In the open cones the tips of the ovules are exposed for a few days before pollination drops appear in the micropyles.

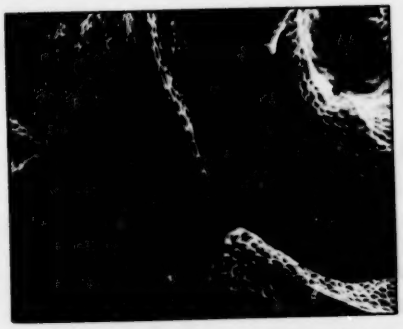


FIGURE 33. Scanning electron micrograph of a western redcedar cone showing the bract-scales (B) and ovule micropyles (M) with and without pollination drops (PD). (X 80)

FIGURE 34. Scanning electron micrograph of a yellow-cedar seed cone showing the bract-scales (B), and ovules, some with pollination drops (PD). (X 45)

In both species, pollen landing on an ovule tip that lacks a pollination drop will usually adhere to the ovule tip, and be taken into the pollination drop when the latter is exuded. Pollen landing on an ovule tip that does have a pollination drop, sinks immediately into the drop, leaving marks on the surface of the drop where it entered (Fig. 35). This apparently alters the surface tension of the pollination drop, which is then rapidly withdrawn (within approximately 30 minutes) (Fig. 36), carrying the pollen into the micropyle (Fig. 37).

FIGURES 35-37. Scanning electron micrographs of yellow-cedar ovule tips showing the pollination drop just after pollen has entered leaving marks on the surface (FIGURE 35) (X 190), withdrawl of the pollination drop (FIGURE 36) (X 300) and the pollination drop completely withdrawn, leaving some pollen on the rim and within the micropylar canal (FIGURE 37). (X 380)

Pollination drops in the two species are secreted by the cells of the nucellus. The drops, more viscous than water, contain small amounts of sugars. Large pollination drops may fuse between ovules or touch and adhere to the surface of the scale (Fig. 33), providing a large surface area on which pollen can land. Large drops may pick up pollen adhering to the ovules or bracts.

Tiny rain or dew drops do not wet the surface of the bracts as they do leaves. Instead, they form tiny beads that are funnelled down the bract surface to the ovules, where they fuse with pollination drops. Those water drops may pick up pollen that adheres to the bract surface, and carry them to the ovule. The reason water beads on the bract surface is that the bract is covered with minute waxy rods that prevent the drop from touching a flat surface. Leaves on the same plants have much shorter waxy rods and are therefore readily wetted by rain water.

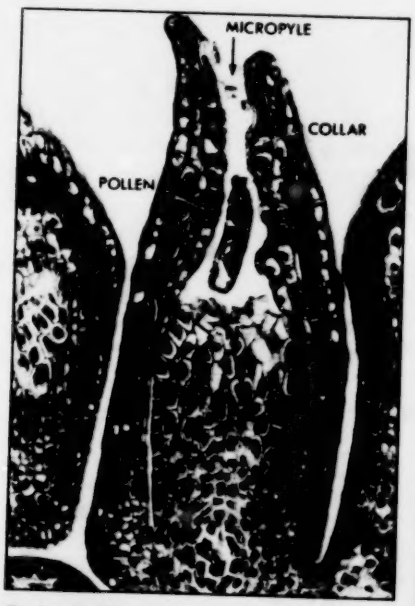


FIGURE 38. Median longitudinal section through a yellow-cedar ovule. The pollen is elongating and cells lining the micropylar canal have started to form the collar. A large megaspore mother cell (MMC) is at the base of the nucellus (N). (X 130)

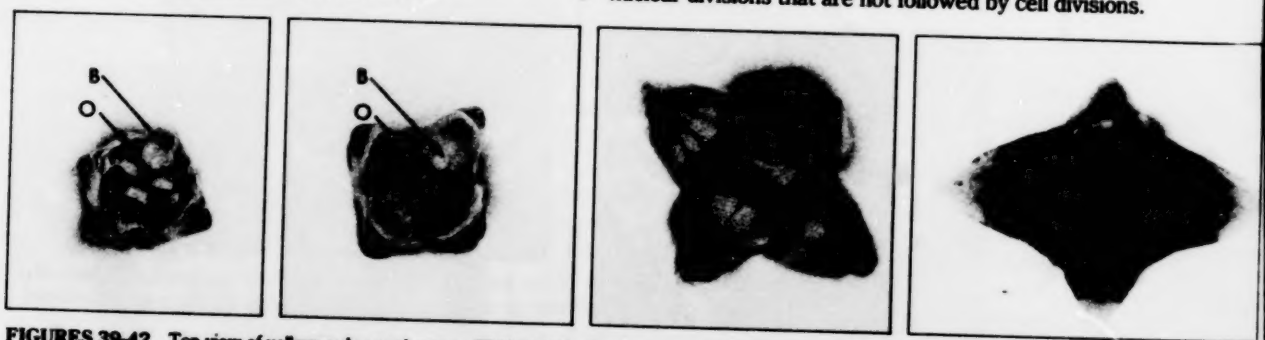
Pollen that enters a pollination drop directly, or enters via a rain or dew drop, is carried into the micropyle when the pollination drop evaporates and is withdrawn into the ovule. After the final withdrawal of the pollination drop, cells lining the micropylar canal divide and enlarge, forming a collar that seals the micropyle (Fig. 38). After approximately one week of receptivity (Fig. 39), bracts begin to enlarge rapidly (Fig. 40), overgrowing (Fig. 41) and burying the ovules deep within the cone (Fig. 42).

The most effective pollination may be accomplished if pollen arrives before or during pollination drop exudation. Pollen arriving after the last pollination drops are withdrawn is not likely to enter the tiny micropyle before it is sealed. Pollen arriving before pollination drop exudation may be picked up by the drop. Light rain or dew can aid pollination by picking up pollen from the bract surface and carrying it to the pollination drop. As well, rain or dew increases the pollination drop surface by fusing with the drop.

Because only a few ovules are receptive at any one time, the pollination mechanism of western redcedar and yellow-cedar appears to be well adapted to conditions where small amounts of pollen are shed over several days. Also, both species are best adapted to wet, humid climates where pollination can occur very early in the spring, within a few days or weeks after dormancy ends.

Ovule Development

Ovules in dormant seed-cone buds of both western redcedar and yellow-cedar each contain a single large megaspore mother cell buried deep in the nucellus (Figs. 38, 44*A*). Soon after dormancy ends the megaspore mother cell enlarges and, within approximately one month, divides by meiosis to form four megaspores, each with half the original number of chromosomes. The three outer megaspores degenerate while the fourth megaspore enlarges (Fig. 44*B*), becomes vacuolate, and begins a series of free nuclear divisions that are not followed by cell divisions.



FIGURES 39-42. Top view of yellow-cedar seed cones. **FIGURE 39.** Seed cone opening and receptive showing ovules (O) and bract-scales (B). **FIGURE 40.** Seed cone receptive but bract-scales have begun to enlarge. **FIGURE 41.** Bract-scales enlarged and starting to cover ovule. Cone is no longer receptive. **FIGURE 42.** Bract-scales have enlarged and buried the ovules. (X 7)

An irregular sac-like female gametophyte forms, consisting of a thin parietal layer of multinucleate cytoplasm and a large central vacuole (Figs. 43, 44*C*). The female gametophyte is bounded by the megaspore

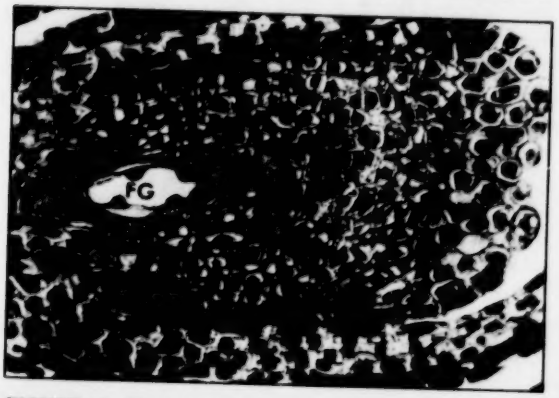


FIGURE 43. Western redcedar ovule showing the free-nuclear female gametophyte (FG). (X 25)

wall. Outside this wall is a spongy tapetum (Figs. 44*C*, *D*) that degenerates during female gametophyte development, adding to the thickness and sculpturing on the surface of the megaspore wall. The method is similar to the degeneration of the tapetum in the microsporangium, which contributes to the exine and sculpturing of the pollen wall.

The ovule and female gametophyte enlarge for approximately one month, then cell walls form rapidly, dividing the female gametophyte into many large cells (Fig. 44*D*), most of which divide in turn. Thus the female gametophyte enlarges and the large central vacuole (Fig. 45) is replaced by many small cells (Fig. 44*E*). At the micropylar end of the female gametophyte several cells do not divide, but elongate and function as archegonial initials (Figs. 44*D*, *E*, 45). Without any small cells remaining between the archegonial initials, a single archegonial jacket layer develops around the group of archegonial initials, commonly 10 per jacket (though it can range from 5 to 20) (Fig. 47). Together the archegonial initials and archegonial jacket develop into the archegonial complex characteristic of the Cupressaceae.

Each archegonial initial enlarges, becomes vacuolate, and divides unequally, producing a small primary neck cell at the micropylar end, and a large vacuolate central cell (Fig. 44*F*). Each primary neck cell divides to form one layer of four to six neck cells (Fig. 46). The large vacuole of the central cell fills in

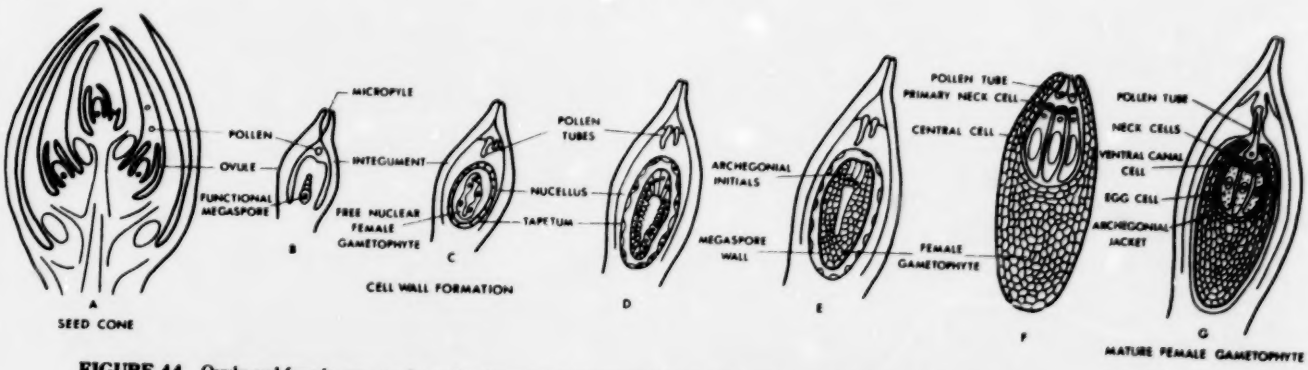


FIGURE 44. Ovule and female gametophyte development of western redcedar and yellow-cedar following dormancy. *A* represents the dormant seed cone. *B-E* show sections of ovules. *F* shows only the female gametophyte. *G* shows the ovule containing the mature female gametophyte within the ovule.

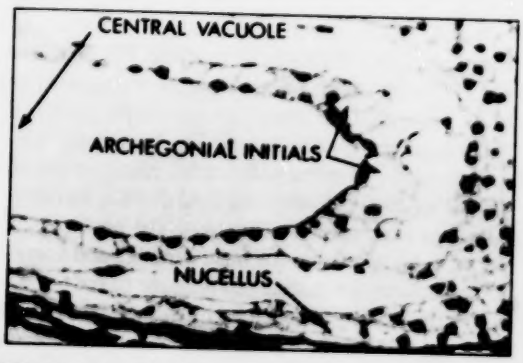


FIGURE 45. Western redcedar ovule showing the archegonial initials within the female gametophyte. (X 230)

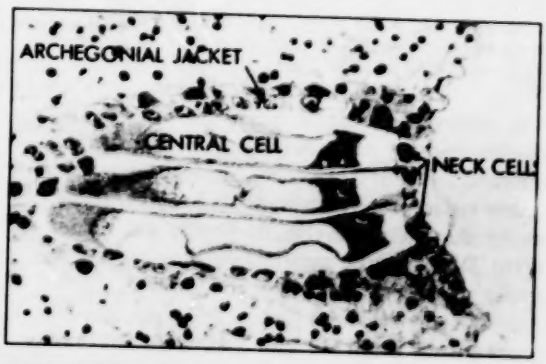


FIGURE 46. Median longitudinal section of a western redcedar female gametophyte containing an archegonial complex. (X 230)

and the central cell divides unequally, forming a large egg cell and a small, inconspicuous ventral canal cell adjacent to the neck cells (Figs. 44*G*, 48). The egg cell cytoplasm develops storage products as large proteid bodies. At this point the female gametophyte is mature and ready for fertilization (Figs. 44*G*, 48).

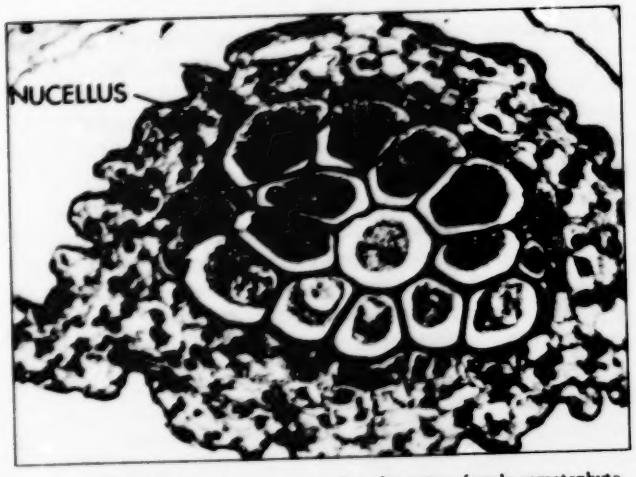


FIGURE 47. Transverse section of a mature female gametophyte of yellow-cedar showing 13 archegonia within the archegonial complex. (X 200)

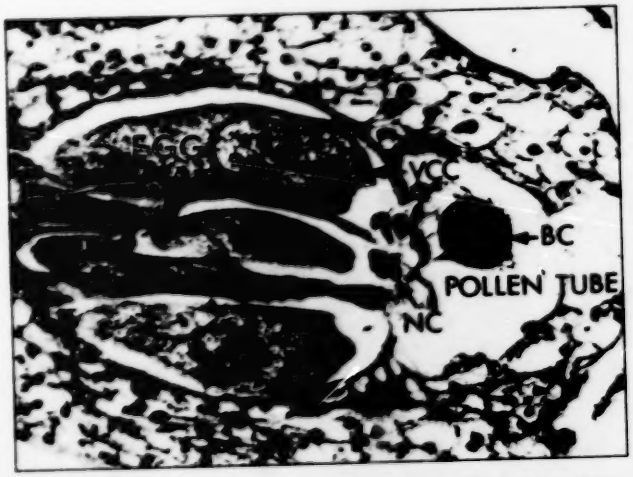


FIGURE 48. Median longitudinal section of a yellow-cedar mature female gametophyte after penetration of the pollen tube which contains the body cell (BC). Each archegonium contains neck cells (NC), ventral canal cells (VCC) and an egg. (X 130)

In western redcedar the female gametophyte reaches maturity in late May, about 11 weeks after pollination (Fig. 5) (Owens and Molder 1980); and in yellow-cedar it reaches maturity in late July, about 12 weeks after pollination (Fig. 6) (Owens and Molder 1975). During female gametophyte development the ovules and seed cones enlarge to what is approximately their final size. At this stage, seed cones are still green and have not yet become hard or woody. Western redcedar cones remain erect, whereas yellow-cedar cones are pendant.

Fertilization

In both species, pollen taken into the micropyle may be drawn to the tip of the nucellus, or it may adhere to the surface of the micropylar canal. As the collar forms and seals the micropylar canal, the tips of the micropyle wither and the nucellus grows along the canal, reaching some of the pollen adhering to the surface. In yellow-cedar, some of the pollen that does not come in contact with the nucellus germinates, shedding the exine and elongating along the micropylar canal (Fig. 38). The elongated pollen is not the pollen tube that forms after the elongated pollen reaches the nucellus. This process of pollen elongation before pollen-tube formation has not been observed in western redcedar, but it does occur in other conifers, such as Douglas-fir and larch.

When pollen grains reach the nucellar tip, they settle into the depression created by the degeneration of a few nucellar tip cells (Fig. 38). Several pollen tubes, one from each pollen grain, begin to develop soon after pollination. Large pollen tubes usually reach the female gametophyte at about the time the central cell divides to form the ventral canal cell and the egg cell (Figs. 44, 48).

FIGURE 49. Median longitudinal section of a mature yellow-cedar female gametophyte showing the archegonial complex, the two male gametes (MG) and several groups of neck cells (NC). (X 150)

During pollen tube growth, the generative cell of the pollen grain divides to form a stalk cell and a body cell. After the pollen tubes reach the archegonial neck cells, the tips of the tubes flatten over the neck cells and a large cavity often forms. The large body cell moves to the tip of the pollen tube, just over the neck cells (Fig. 48). The body cell then divides, forming two large male gametes (Fig. 49). The neck cells become disrupted and the male gametes and some of the cytoplasm are discharged into one of the archegonia. Several pollen tubes may be present and each can enter a separate archegonium. The presence of an archegonial complex, where neck cells of separate archegonia are contiguous (Fig. 49), makes it

feasible for two male gametes from one pollen tube to enter separate archegonia. This, however, has not been observed in either western redcedar or yellow-cedar. Usually one male gamete fuses with the egg nucleus, while the second male gamete remains near the neck of the archegonium (Fig. 50*A*). A receptive vacuole results from the discharge of the pollen-tube contents into the egg cytoplasm. Generally several eggs per ovule are fertilized. Unfertilized eggs degenerate soon after the time of fertilization which in western redcedar, occurs in late May, about 11 weeks after pollination; and in yellow-cedar in late July, about 12 weeks after pollination (Owens and Molder 1975, 1980).

Embryo Development

As in other conifers, embryo development in the Cupressaceae is separated into two phases: first a proembryo phase, which occurs within the archegonium; and later an embryo phase, which occurs after the proembryo elongates into the female gametophyte tissue.

Proembryo development in western redcedar is similar to that in other species of *Thuja*, but differs from that of yellow-cedar. Some variation occurs within each species and this can result from the variable sizes of the archegonia within the archegonial complex. Some female gametophytes can have several

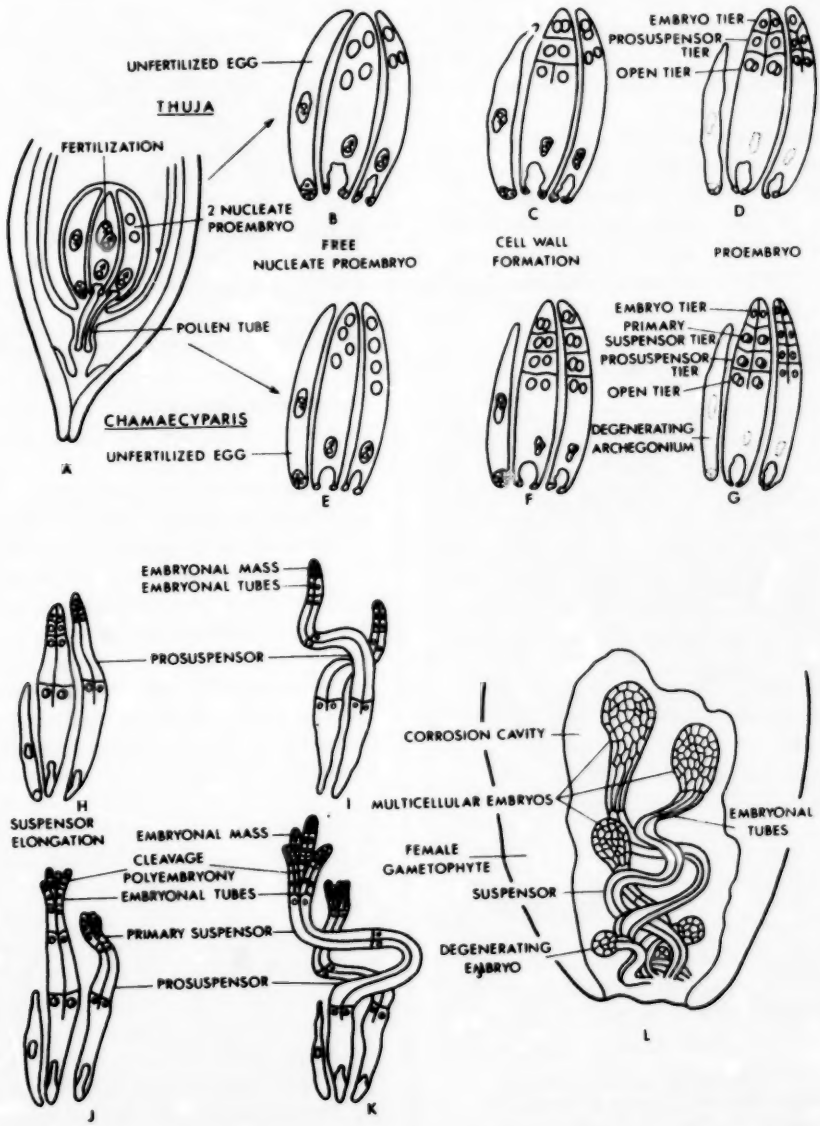


FIGURE 50. Early embryo development in western redcedar (upper series) and yellow-cedar (lower series). *A* and *L* appear similar in both species. *B-G* shows proembryo stages and *H-K* shows early embryo stages.

narrow archegonia, whereas others will have only a few broad archegonia. Long narrow archegonia limit the direction in which nuclei and cells divide, but broad archegonia allow varied forms of development. In both species the nucleus of the fertilized egg, or "zygote", divides to form two nuclei, but no cell wall separates them (Figs. 50*A*, 51). Usually, each of these nuclei divides and four nuclei are formed in various arrangements in the distal half of the archegonium (Figs. 50*B*, *E*, 52).

In western redcedar occasionally only one of the nuclei divides, resulting in three free nuclei in a triangular arrangement (Fig. 50*B*). Cell walls may form at this time, or after some or all of the nuclei divide once more (Fig. 50*C*). Generally, western redcedar will form a three-tiered proembryo including a basal "open tier", having four cells open to the egg cytoplasm; a middle "prosuspensor tier", having four cells; and a distal "embryo tier", having one or two cells (Fig. 50*D*).

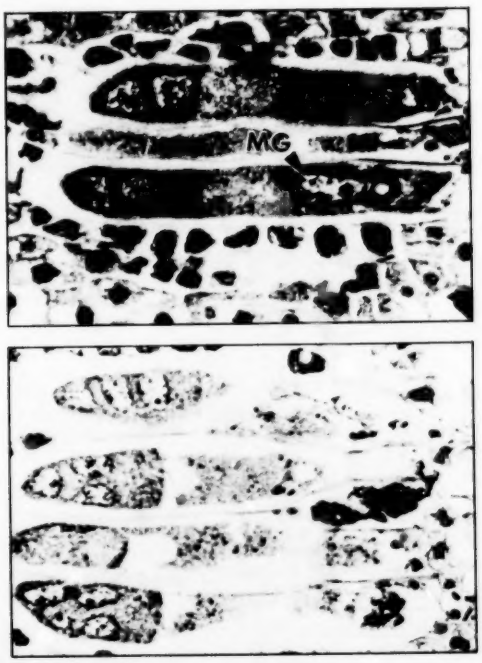
In yellow-cedar, the zygote nucleus divides without cell wall formation, and each nuclei divides to form a single file of free nuclei in the long slender archegonium (Fig. 50*E*). After transverse cell walls form (Fig. 50*F*), the cells usually divide twice, forming a four-tiered proembryo, generally with four cells per tier (Fig. 50*G*). These tiers are: the "basal tier", which is open to the egg cytoplasm; the adjacent "prosuspensor tier"; the primary "suspensor tier"; and lastly the distal "embryo tier" (Fig. 50*G*). Despite the various forms of proembryo development for species of Chamaecyparis (Johansen 1950; Wardlaw 1955), all result in a four-tiered proembryo with a variable number of cells in each tier (Fig. 50*G*).

Proembryo development is complete in both species approximately one week after fertilization (Figs. 50*D*, *G*). Often more than one proembryo forms in an ovule. Because each embryo normally results from the fusion of an egg nucleus with a male gamete from a different pollen tube, each proembryo is genetically different from the others. This is called "simple polyembryony".

As soon as the proembryo is formed, the prosuspensors elongate, forcing the distal cells into the female gametophytic tissue (Figs. 50*H*, *J*). The distal embryo tier then divides, forming files of cells (Figs. 50*H*, *J*). In yellow-cedar, it is usually four files of cells that form and separate (Fig. 50*K*). Each file may develop into an embryo that is genetically identical, a process called "cleavage polyembryony". In western redcedar cleavage polyembryony is not observed because, even though the distal tier divides to form two or more files of cells, the files do not separate (Fig. 50*I*).

In both western redcedar and yellow-cedar, the elongating prosuspensors thrust the distal cells into the female gametophytic tissue, at the same time buckling to form a tortuous maze of tubular cells between the developing embryos and the collapsing archegonia (Figs. 50*I*, *K*). The prosuspensor cells and elongating primary suspensor cells may divide at their distal ends, forcing the distal cells even further into the female gametophyte (Fig. 50*L*).

In western redcedar, one or more embryo cells at the tip of the prosuspensors (Figs. 50*D*, *H*) divide to form a single embryonal mass (Fig. 50*I*). Although a multicellular embryo may develop from each archegonium, usually only two or three multicellular embryos form. This stage is usually reached by mid-June, about 13 weeks after pollination (Figs. 50*L*, 53). Embryo development continues and is completed by mid-August (Fig. 5).



FIGURES 51, 52. Median longitudinal sections of western redcedar female gametophytes showing free-nuclear stages of proembryo development. (X 230) Figure 51. Two free nuclei and the remaining male gamete (MG) at the proximal end of one archegonium. Figure 52. Three arrangements of free nuclei are shown. (X 230)

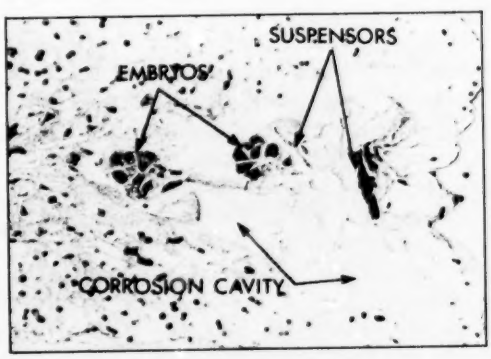


FIGURE 53. Two early multicellular embryos of western redcedar at the ends of coiled suspensors. (X 110)

In yellow-cedar, the embryo cell of each of the four files of cells (Fig. 50*G*) divides, forming a small embryonal mass at the tip of each suspensor (Fig. 51*K*). Because yellow-cedar has both simple and cleavage polyembryony, many small embryos occur normally in each ovule (Fig. 50*K*). The more vigorous embryos enlarge and extend into the female gametophyte. Less vigorous embryos degenerate near the archegonia (Fig. 50*L*), and a small corrosion cavity surrounds them and their coiled suspensors (Figs. 50*L*, 54). This stage is reached early in the fall for yellow-cedar, at which time embryo development stops and seed cones become dormant (Figs. 6, 54).

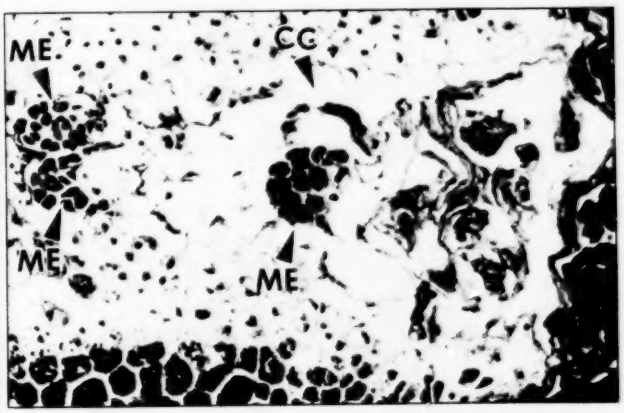


FIGURE 54. Three large and several small multicellular embryos (ME) in the corrosion cavity (CC) of the dormant seed of yellow-cedar. (X 140)

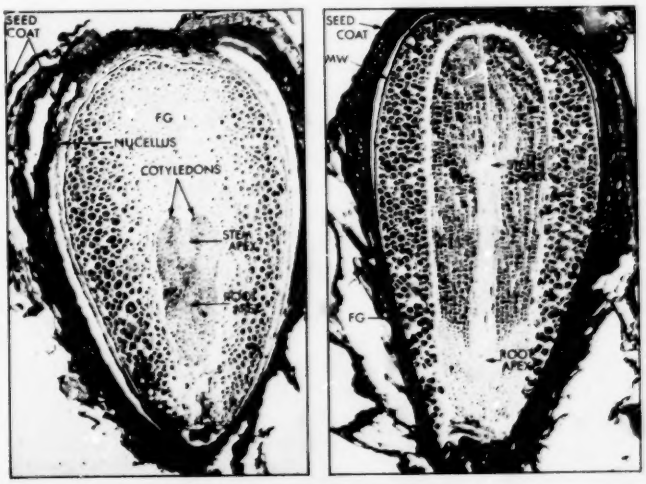
Whether embryo development is completed in one season, as in western redcedar, or occurs over two growing seasons, as in yellow-cedar (Figs. 5, 6), the later stages of embryo development essentially are the same in both species.

Usually it is only the distal, more vigorous multicellular embryo that develops further (Fig. 50*L*), while the others degenerate or remain as small clumps of cells within the female gametophyte. Cell divisions within the remaining multicellular embryo are frequent, and at first occur in all directions, resulting in a large, club-shaped embryo in the centre of the female gametophyte. As cell divisions become less random, distinct meristematic regions appear. In the proximal region a root apex is formed, developing the root cap and contributing cells to the suspensor system. In the distal region, two cotyledons are initiated, with a small shoot apex between (Fig. 55). The axis elongates between the root and shoot apices and a long root tip forms before the embryo matures and becomes dormant. In western redcedar this occurs in mid-August, five months after pollination (Fig. 5); in yellow-cedar it occurs the following July or August, 15 to 16 months after pollination (Figs. 6, 56). Throughout embryo development a corrosion cavity forms within the female gametophyte, around the embryo. The mature embryo within this cavity nearly fills the female gametophyte, as both embryo and female gametophyte become stored with starch and other foods during development (Fig. 56).

The Seed

The two lateral ridges that form on the ovules before pollination (Fig. 34) enlarge during ovule development. They appear on the ovules, whether or not pollination and fertilization have occurred, and form the small lateral seed wings (Figs. 58, 60) characteristic of the Cupressaceae.

Near the time of fertilization, the ovule integument begins to differentiate into the seed coat. In western redcedar the seed coat is thinner than that in yellow-cedar, but both develop in the same way and contain the same tissues in three layers. The outer layer is very thin and brown. The thick middle layer is hard, stony, and especially thick beneath the seed wings. The thin inner layer lies adjacent to the nucellus (Fig. 55). Ovules remain attached to the cone axis during early development but separate from it after food has been stored in the female gametophyte and the embryo has begun to develop.



FIGURES 55, 56. Median longitudinal section of yellow-cedar seeds. FIGURE 55. Immature seed collected in the summer showing the developing embryo in the female gametophyte (FG). (X 50) FIGURE 56. Mature seed. (MW, megaspore wall). (X 50)

In the mature seed, the embryo is loosely packed within the firm, brown female gametophytic tissue. This tissue, containing abundant stored food, functions as a food reserve for the developing embryo and the young germinating seedling. A thin megaspore wall encloses the female gametophyte (Fig. 56). In most seeds the nucellus is not visible, although it can sometimes be seen at the ends of the seed, between the megaspore wall and the seed coat.

Western Redcedar Cone Maturation, Seed Release, and Regeneration

Approximately 16 months elapse between pollen-cone and seed-cone initiation, and the shedding of mature seed (Fig. 5). Seed cones are fully enlarged but still green and non-woody at the time of fertilization in early summer. Seed cones remain erect during maturation. In late summer the bract-scales become woody and turn brown (Fig. 57).

Seed cones dry and open in early fall. Dry, warm weather in late summer can cause faster drying and earlier opening of the cones, and, hence earlier seed release. Wet, cool weather can delay seed release. Although most seed is shed in the late summer or fall, some may be retained in the cones and shed throughout the winter. In the coastal region, peak seed-fall occurs during November. The best time to collect mature cones is from late August through early September. Cones that turn brown and open prematurely often have been damaged by insects and contain few or no filled seed.

Western redcedar is a prodigious seed producer. Although its seed cones bear only a few seeds, each tree can produce abundant seed cones. These cones have four or five (rarely six) pairs of bract-scales (Fig. 57). The proximal two often bear rudimentary ovules that seldom develop into seeds; the next four usually bear three ovules each; and the two distal bract-scales usually bear only two ovules each. If other more distal bract-scales are present, they are rudimentary and bear no seeds. Consequently, the total seed set potential of a cone at pollination is only about 16 ovules in the axils of the three middle pairs of bract-scales.

FIGURE 57. Mature western redcedar seed cones. (X 1)

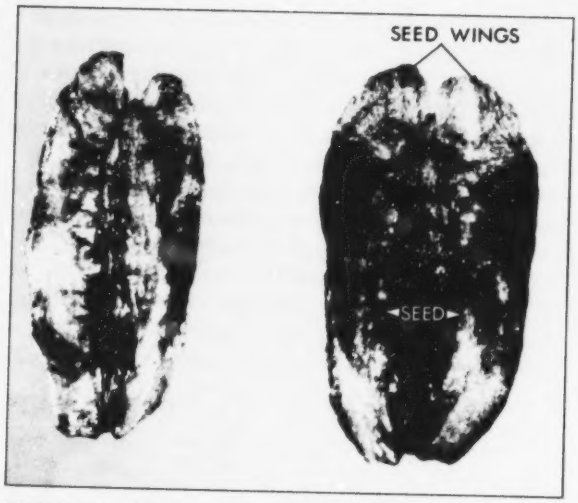


FIGURE 58. Mature western redcedar seed. On the left is the upper surface and on the right is the lower surface (adjacent to the bract-scale). (X 20)

Approximately 20 percent of these ovules abort very early, at or shortly after pollination, and disappear or remain as rudimentary structures in the mature cone. These ovules commonly are those in the axils of basal and distal bract-scales and are poorly developed at the time of pollination. Cold temperatures at pollination also appear to cause ovule abortion in fertile regions of the cone. Of the 16 potential seeds per cone, about 40 percent are empty early, due either to abortion of the megaspore, or to abortion during female gametophyte development. The incidence of this early ovule abortion and abnormal, sterile ovules is higher in cones infested by the redcedar cone midge (*Phytophaga thujae*). Other unknown factors are also involved. About 25 percent of the potential seeds contain spongy female gametophytic tissue but no embryos. These appear to result from either no pollination or from embryo abortion. These seeds are of normal size, but the seed coats are often thin and discoloured. The thin seed coats and spongy contents result in soft seeds, distinguishable from those that are filled. Only about 15 percent of the ovules (2.6 seed/cone) develop into filled seeds containing mature embryos (Fig. 58).

Many cones abort either at or shortly after pollination, and then wither and fall from the branch. This is thought to be caused by low temperatures. Other cones with less severe damage develop normally only to have all their ovules abort later. Cones containing heavy insect infestations are usually broader and more swollen than normal cones, and

larvae are readily visible when cones are broken open (Owens and Molder 1980).

The seed of western redcedar, though small and light, has small seed wings (Fig. 58). Consequently, the rate of seed fall is fast and the distance of wind dispersal is not great — usually not more than 120 m from the source (Fowells (compiler) 1965).

Western redcedar trees can produce seed when they are fairly young (15 years) and cone crops are frequent. Poor cone crops rarely occur (Fowells (compiler) 1965). This factor, plus the abundant cones per tree, offset the poor seed set per cone and the limited dispersal. In a mature forest, abundant western redcedar seed is produced compared with its associated species, except western hemlock; and the small seed is eaten less by rodents than is the larger seed of other conifers (Fowells (compiler) 1965). These factors make western redcedar potentially good for natural regeneration.

Fall seed germination and seedling establishment are common in coastal regions, depending upon local weather conditions. Spring seed germination and seedling development are more common in interior regions. Under natural conditions germination percentage is high compared with that of most associated species. Germination of western redcedar seed is better on burned or unburned mineral surfaces than on duff (Fowells (compiler) 1965).

The present methods used for commercial seed extraction and seed germination for western redcedar are as follows. Stored cones are kiln dried for 18 to 20 hours at 41°C. Slightly lower temperatures may be used if cones have already begun to open. Most seeds will be released from the cones during the drying or during the subsequent tumbling of dried cones. Seeds require no pre-chill period. The best germination is obtained if seeds are soaked for 24 hours in water, blotted dry, and placed at 20-30°C with 8 hours of light and 16 hours of dark per day for 21 days[1].

Seedling mortality is very high in western redcedar. Early losses to fungi, birds, and insects are common. In full sunlight few seedlings survive the high soil surface temperatures. They survive best in partial shade (Fowells (compiler) 1965).

Western redcedar seedlings have two cotyledons. After seed germination, the shoot apex produces many short primary needle-like leaves, three to a whorl. Usually during the first growing season, some lateral branches are initiated, forming the scale-like, decussate leaves and flattened branches characteristic of the mature plant (Fig. 61).

[1]British Columbia Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

Yellow-cedar Cone Maturation, Seed Release, and Regeneration

Approximately 28 months elapse between pollen-cone and seed-cone initiation, and the shedding of mature seed (Fig. 6). Seed cones are fully enlarged but still green and non-woody soon after fertilization occurs (Fig. 59). When 1-year-old seed cones overwinter at this stage, they contain only immature embryos (Fig. 54). During the third growing season, the 2-year-old seed cones become hard and woody and change from green to yellow (Fig. 59).

Because embryo and seed development take place during the two years after pollination, both immature (1-year-old) and mature (2-year-old) seed cones can occur on the same branch (Fig. 4). This can result in a collection of immature cones that will not yield viable seed. Several criteria can be used to distinguish mature from immature cones and seeds. Immature cones are normally found close to the tip of the branch, while mature cones occur further from the tip (Figs. 4, 59). If only one year's cones are present on a branch, it is more difficult to determine the age of the cone. Mature and immature cones may be equal in size (6 to 13 mm in diameter). Immature cones are green, often with some purple, and they are soft and easily opened using fingernails. Mature cones are yellow-green, often with dark brown spots, and they are hard, not easily opened using fingernails. As well, the lines between their scales are distinct and raised. Seeds from immature cones are white, soft, moist, and not viable. Seeds from mature cones are dark brown, hard and dry (Fig. 60) (Owens and Molder 1975).

FIGURE 59. Immature (1-year-old) yellow-cedar seed cones on the left, and mature (2-year-old) seed cones on the right. (X 5)

FIGURE 60. Mature yellow-cedar seed. On the left is lower surface (adjacent to the bract-scale), and on the right is the upper surface. (X 15)

Mature, 2-year-old seed cones dry, turn from yellow to brown and open in late September. After seeds are shed (most in October; the rest during the winter), mature cones usually fall from the trees. The best time for cone collection is generally from mid-September to mid-October. Some disease- or insect-damaged immature cones may cause cells to proliferate where the bracts join, causing the scales to separate prematurely, change colour, and appear to be like mature cones in the process of opening (Owens and Molder 1975).

Yellow-cedar is not as prodigious a seed producer as is western redcedar. Although yellow-cedar can produce some mature cones every year, moderate to good cone crops occur only every two to four years (Fowells (compiler) 1965). Usually, each seed cone has only four bract-scales, each with two or three axillary ovules. Occasionally a fifth or sixth bract-scale is present, but these normally lack ovules. Consequently, the seed set potential is only about 8 to 12 seeds per cone (Owens and Molder 1975), with the average being 7.

Despite these numbers, the proportion of filled seed per cone averages only two, or approximately 30 percent. The causes of empty seeds are uncertain and difficult to determine in such a long reproductive cycle. Some ovules abort near the time of pollination and degenerate. Others abort before fertilization and remain as small, empty seeds. Some appear not to have been pollinated at all, or to have been pollinated but suffered embryo abortion. In this case the seeds look normal (because pollination is not necessary for ovule development), but their seed coats are thin and the contents are dry and spongy. Many cones appear to stop development after pollination, and either remain on the tree as small, arrested cones or drop from the branch (Owens and Molder 1975).

The frequent abortion and arrested development of ovules and young cones may be the result of the low temperatures that often occur near the time of yellow-cedar pollination at higher elevations. Also, the tree may have a limited capacity for carrying cones to maturity, since arrested cones are very common on branches bearing many seed cones (Owens and Molder 1975).

Yellow-cedar seed, compared with that of western redcedar, is slightly larger, with larger seed wings, and heavier (Figs. 58, 60). The rate of seed fall is fast and the distance of wind dispersal is normally less than 120 m (Fowells (compiler) 1965).

The regenerative capacity of yellow-cedar under natural conditions is relatively low, but the causes for this are not well understood. The poor seed set and relatively few cones produced per year may explain why so few seedlings are found in nature. It is slow growing and less shade tolerant than many of its associated species. Consequently, it competes well only on sites less favourable for the usual associated species — western redcedar, western hemlock and Sitka spruce (Fowells (compiler) 1965).

Yellow-cedar seed requires a long cold period to germinate and therefore spring germination and seedling establishment are common. Seedlings have two cotyledons, and the shoot apex produces many short, primary, needle-like leaves, three to a whorl. During the first growing season, or more commonly later, lateral branches are initiated forming scale-like, decussate leaves and flattened branches characteristic of the mature plant (Fig. 62).

FIGURE 61. One-year-old nursery-grown western redcedar seedling. (X 5)

FIGURE 62. One-year-old nursery-grown yellow-cedar seedling. (X 5)

The present methods used for commercial seed extraction and seed germination are as follows. Stored cones are kiln dried for 18 to 20 hours at 33°C. Most seeds will be released from the cones during drying or during the subsequent tumbling of dried cones. The best germination is obtained if seeds are soaked for 24 hours in water; blotted dry and incubated at 20 to 30°C for 30 days; placed in the dark at about 2°C for three to six months; and, finally, kept at 30°C during the day (8 hours) and 20°C during the night (16 hours) until germination occurs[1].

Yellow-cedar is well adapted to its habitat. By spreading embryo and seed development over two growing seasons it is able to reproduce in severe climates where the growing season is short. Pollen development in the fall, before dormancy, allows the species to pollinate very soon after dormancy ends, thus making the best of a short growing season. The long stratification requirement for seed germination is well adapted to the long winters and early snows common throughout much of its range.

[1]British Columbia Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

Summary

The reproductive cycle of western redcedar is similar to that of most conifers whose cone initiation occurs the first year, and pollination, fertilization, and ovule and seed development occurs the second year. Although cone initiation in yellow-cedar takes place at about the same time and in much the same way as in western redcedar, the remaining portion of the reproductive cycle spans two growing seasons. Pollination, fertilization and early embryo development occur in the second year; while complete embryo development, following a winter's endurance, occurs in the third year. Many aspects of the reproductive cycle of yellow-cedar make it well adapted to a severe climate and short growing season, whereas the reproductive cycle of western redcedar is better adapted to a milder climate and longer growing season.

Pollen cones and seed cones of both species can be induced, even in seedlings, with a simple and inexpensive hormone treatment. Seed produced by these cones is viable.

Cone induction and better understanding of the complete reproductive cycle of both western redcedar and yellow-cedar are important steps toward the development of tree improvement programs and the production of seed for reforestation.

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